

# Rates and Processes of Compensatory Buoyancy Change in *Nautilus macromphalus*

by

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*Abstract* When faced with sudden buoyancy gain or loss, specimens of *Nautilus macromphalus* undergo compensatory buoyancy change. Rates of compensatory buoyancy change (as measured by weight gain or loss in seawater) depend upon animal size and the amount of initial buoyancy change; the higher the initial buoyancy gain or loss, the higher the compensatory buoyancy change rates. For the experiments described here, the mean rate of compensatory buoyancy change during the first 10-h period following the initiation of the experiment was 0.15 g/h of weight gain for those mature *N. macromphalus* made suddenly more buoyant, and 0.10 g/h of weight loss for the nautilus made suddenly less buoyant. During subsequent 10-h periods, the rates of weight gain for the initially buoyant animals dropped to less than 0.05 g/h, while rates for the initially heavy animals stayed approximately the same. The ultimate amount of weight change for highly buoyant nautilus was limited to about 5 g of in-seawater weight increase, whereas the weight loss in the animals made artificially heavy was unlimited, as long as there was cameral liquid in the chambers to be removed. Positive buoyancy of as little as -5 g was sufficient to trap a mature *N. macromphalus* at the surface, so that no amount of swimming would allow resubmergence.

## INTRODUCTION

THE PHRAGMOCONE of an ectocochliate cephalopod serves to reduce the overall density of shell and animal to approximately that of seawater (DENTON & GILPIN-BROWN, 1966). It has been proposed that an additional function of the phragmocone is to produce buoyancy change on demand, either for vertical migration or for compensatory buoyancy change (HEPTONSTALL, 1970; MUTVEI & REYMENT, 1973). The latter, compensatory buoyancy change, can be defined as density change or buoyancy change brought about by the animal in response to some sudden addition or reduction in the animal's specific gravity. HEPTONSTALL (1970) used, as an example, the case of the ammonoid *Buchiceras bilobatum*, which, during life, became covered with oysters (first described by SEILACHER, 1960). Heptonstall showed that the overgrowth of oysters on the shell of the living ammonite would have required compensatory action by the ammonite, in this case a reduction of overall shell density, to maintain neutral buoyancy. Other, perhaps more common examples requiring compensatory buoyancy change can be readily observed in living *Nautilus*. *Nautilus* shells of all species commonly exhibit healed breaks. In some cases, the scars

of what must have been very large breaks are visible, indicating that at some time during the life of the nautilus, many grams of shell material were suddenly lost (Figure 1). Another type of buoyancy change common in nautilus would come from windfall feeding. Nautilus appear to be opportunistic feeders. In New Caledonia, specimens of *Nautilus macromphalus* are known to eat lobster molts (WARD & WICKSTEN, 1980). The ingestion of molt material makes the nautilus more dense. In both of these examples, the action produces rather sudden changes in the buoyancy of the animal, in the first place making it lighter or less dense, in the second, heavier or more dense. The purpose of this paper is to describe experiments conducted with specimens of *Nautilus macromphalus*, designed to test the potentiality and characteristics of compensatory buoyancy change in *Nautilus* under these types of conditions.

## MATERIALS AND METHODS

Specimens of *Nautilus macromphalus* (the only species used in this study) were captured in baited traps at 150 to 400 m in New Caledonia and then immediately trans-

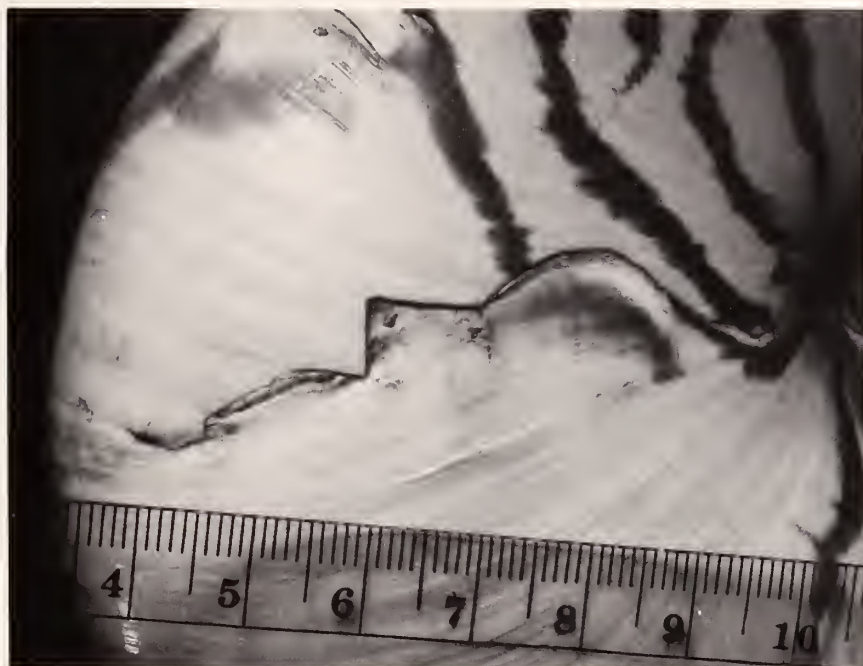


Figure 1

Shell break in *Nautilus* that would have resulted in a sudden loss of buoyancy. Causes of such shell breaks are unknown, but probably result from mechanical impact, predatory attacks, or intraspecific competition.

ported in cooled seawater to a nearby refrigerated seawater system, maintained at 17–18°C. To determine weight in seawater (which will serve as a quantitative descriptor of buoyancy), the nautilus were tightly wrapped in a piece of cheesecloth of known seawater weight, and while still being held underwater, transferred to a submerged rigid plastic box of known seawater weight, suspended by a wire from a modified, electronic top-loading balance (Ohaus Brainweight model 1500). The balance had a sensitivity of 0.1 g. *Nautilus* specimens with densities higher than that of seawater gave positive readings on the balance, while those lighter than seawater gave negative readings. Neutral buoyancy (a nautilus with the density of seawater) zeroed the balance.

Even using the wrapping procedure, the respiratory movements of the nautilus within the closed plastic box sometimes caused sufficient movement to produce a range of weight values. Under these conditions, the balance gave a stream of values, with those considered significant (by the balance) marked by a “g” after the reading. Each data point used in this study is the mean value of 10 stable “g” readings recorded on the balance. The mean standard deviation of 100 randomly selected data points used in this study (1000 balance measurements) was found to be 0.132 g.

Prior to each experiment, the nautilus were fed and radiographed. Except on very long-term experiments (more than 100 h), the nautilus were not fed during the course of the experiments, because feeding significantly increased

weight (both in air and in water). To observe rates of liquid movement into the phragmocone, the last three to five chambers in each specimen were drilled and the cameral liquid volume in each chamber measured or removed using methods described by WARD & GREENWALD (1982). The holes drilled in the chambers were resealed with tapered, hard-rubber stoppers, earlier determined to be leakproof using this procedure (WARD & GREENWALD, 1982). The buoyancy of the experimental animals was then suddenly either increased (by removing shell material from the apertural region with needle-nosed pliers, and in some cases by removing cameral liquid from the first three chambers as well) or decreased (by adding new liquid to chambers, or by adding weights cemented to the side of the shell). To ensure that the drilling procedure was not in some unknown way affecting experimental results, one animal (No. 10) was made more buoyant through shell breakage, but not drilled. This animal showed compensatory weight change similar to those in the drilled animals.

The term buoyancy is used throughout this paper. However, the measures used in this study are weights in seawater and density (specific gravity, determined from weight in seawater and weight in air). In this paper, weight in seawater is used as a descriptor of buoyancy, for lack of a better method of attempting to quantify a qualitative term. A nautilus referred to as 5 g positively buoyant, or 20 g negatively buoyant, refers to specimens weighing –5 or +20 g respectively on the zeroed balance. Animals

showing increasing buoyancy were undergoing reductions of seawater weight and density.

## RESULTS

### Control Experiments: No Induced Buoyancy Change

The weights in seawater of freshly captured nautilus have been previously measured by DENTON & GILPIN-BROWN (1966), WARD *et al.* (1977), and WARD & MARTIN (1978). In every case, the computed densities of the observed specimens have been equal to, or slightly higher than, seawater density (therefore, most display negative buoyancy). In the one study in which weights in seawater were followed through time in aquarium-maintained animals (WARD & MARTIN, 1978), all animals eventually showed increasing buoyancy. In this latter study, however, the weighings were conducted on animals anaesthetized in a 2% solution of urethane in seawater, and maintained in water temperatures of 23 to 26°C. The observations listed here are on unanaesthetized animals kept at cooler temperatures.

The weights in seawater of four freshly captured *Nautilus macromphalus* used in this study are shown in Figure 2. These animals showed a seemingly random fluctuation near neutral buoyancy (0 g). Error bars showing the amount of experimental error (three standard deviations in each direction of a reading) are shown on this graph. No pattern of day versus nighttime weight patterns could be detected. These four animals, without experimentally produced buoyancy change, serve as control animals against which the following experiments and observations can be compared.

### Induced Buoyancy Change: Compensatory Buoyancy Change in Reaction to Increased Buoyancy

To test for the possibility of compensatory change in nautilus made artificially more buoyant, specimens were made suddenly more buoyant by either the removal of cameral liquid, the removal of shell material, or both. This latter procedure mimics the effect of shell breakage, which could occur through either mechanical action (such as impact in shallow water, high energy environments) or predation. Following the episode of increased buoyancy, the nautilus specimens were weighed periodically (generally at 15–30-min intervals during the first 2 h, followed by every one to two hours).

The results of these experiments are shown in Figure 3. In most cases significant weight increases occurred after the initiation of the experiment. Increase in weight (decrease in buoyancy) was usually apparent within the first hour, and sometimes in as little as 30 min. The rate of weight increase was highest during the first 10 h following the initiation of the experiments, and then tapered off, so that most curves of buoyancy change can be seen to descend steeply during the first 10 to 20 h, and then level off after about 30 to 40 h. This suggests that the rate of

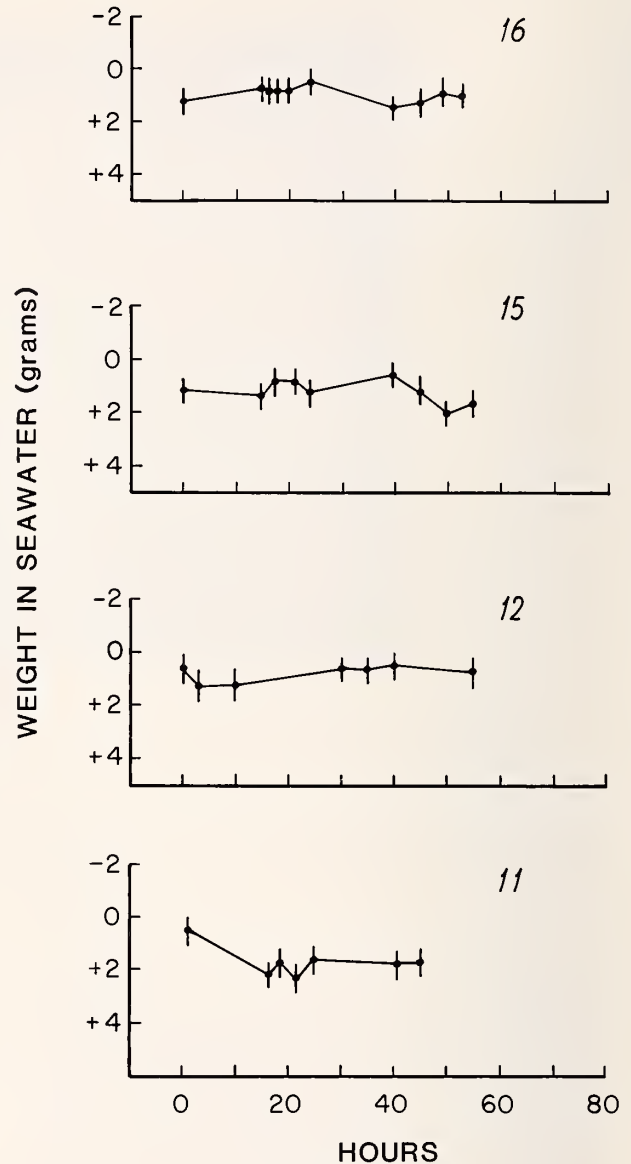


Figure 2

Weight in seawater of four freshly captured *Nautilus macromphalus* (specimens No. 82-16, 15, 12, and 11). The sizes of these animals can be found in Table 2. None of these animals was manipulated in terms of its buoyancy; these measures can, therefore, serve as controls against which the following experiments, involving sudden buoyancy change, can be compared. The vertical bars on the graphs refer to estimated experimental error (0.3 g). Experimental error comes from sensitivity of the balance (0.1 g) and the weighings themselves. Although no subsequent graphs show the error bars, all points listed on subsequent graphs have similar estimated error ranges.

compensatory buoyancy change decreases with time, or has a limit to the amount of change. To test this, mean values for aggregate weight change during 10-h increments following the initiation of the experiments were

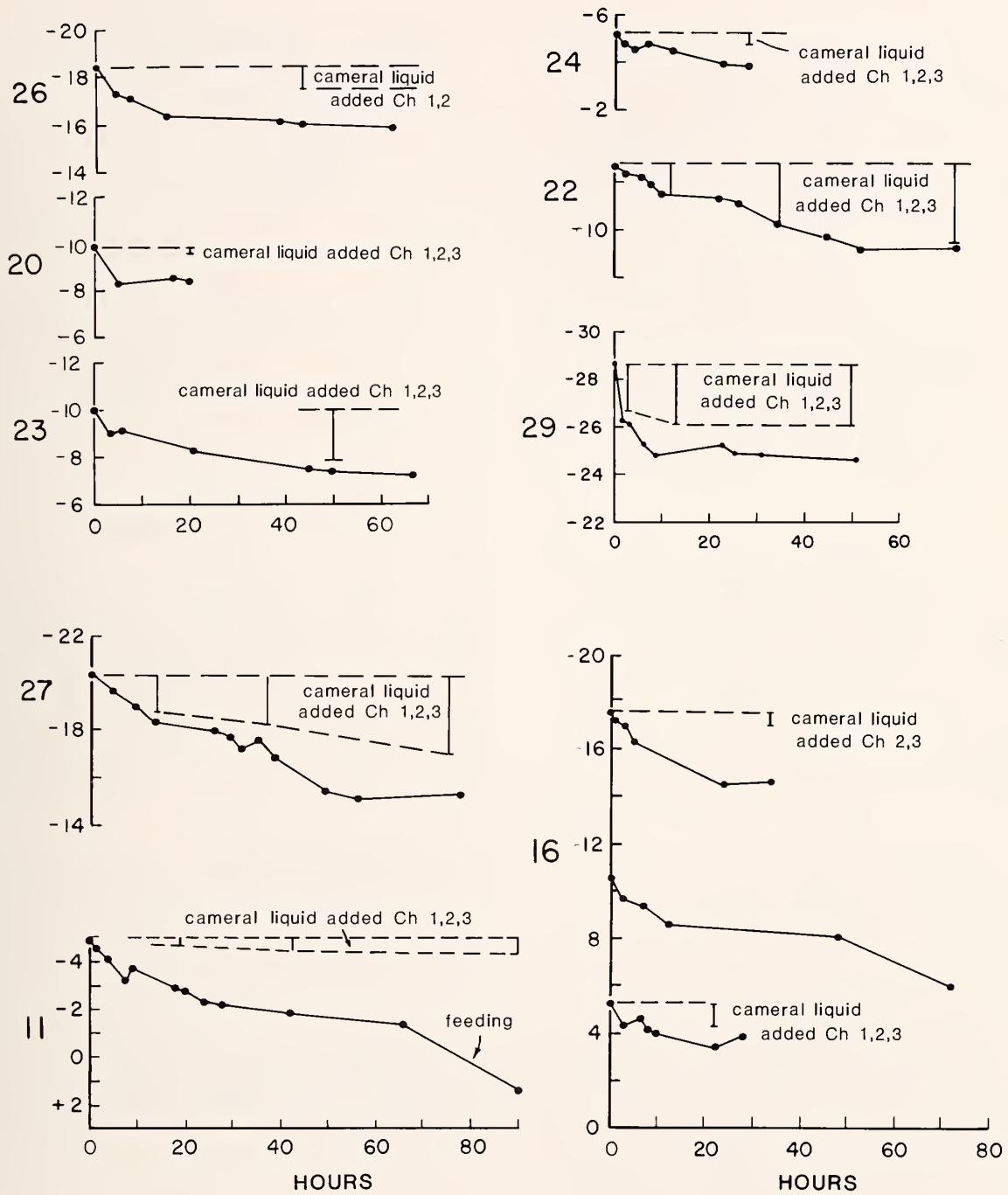


Figure 3

Compensatory buoyancy change in nine *Nautilus macromphalus* made positively buoyant through cameral liquid removal, apertural shell removal, or both. The vertical axis in each graph refers to weight in seawater; the horizontal axes show the number of hours after the initiation of each experiment. The portion of each graph labeled "cameral liquid added" shows the amount of buoyancy change that can be attributed to measurable chamber refilling with cameral liquid.

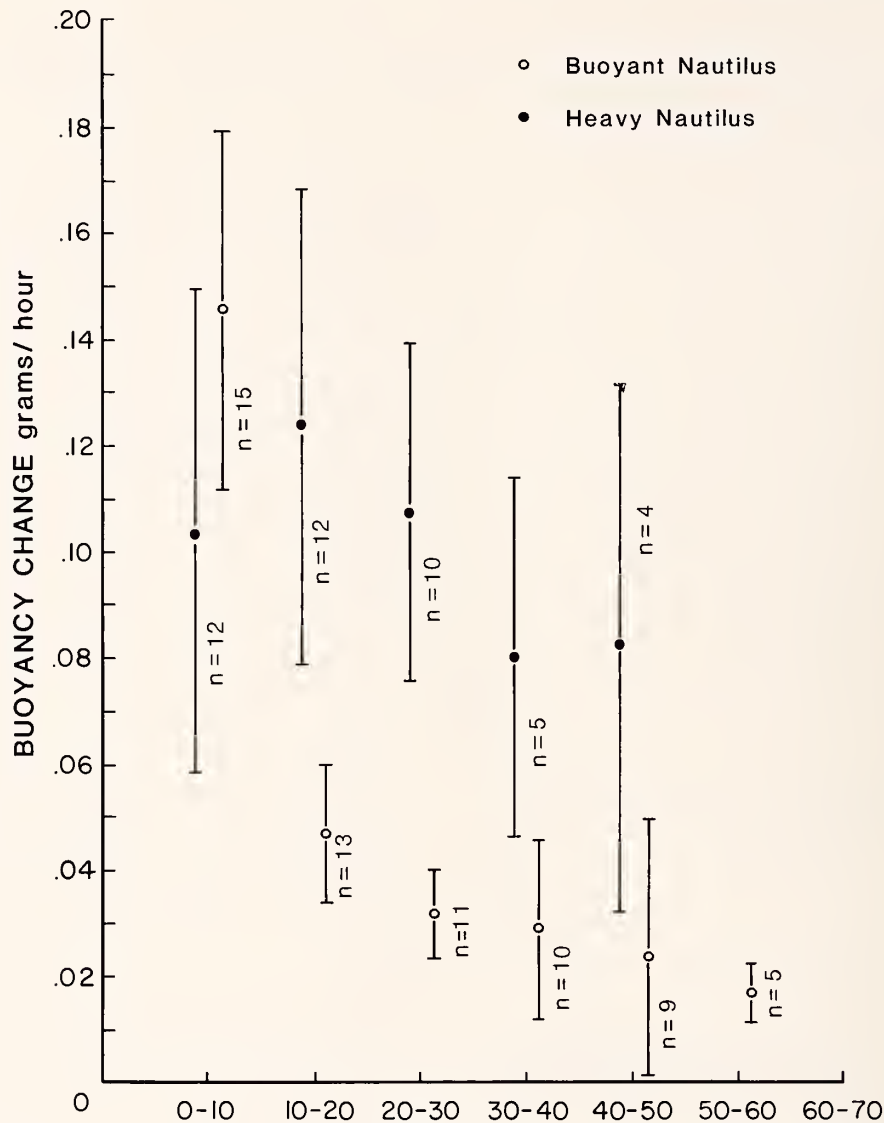


Figure 4

Mean seawater weight changes in 10-h increments for *Nautilus macromphalus* made suddenly positively buoyant (open circles) and negatively buoyant (closed circles). Error bars indicate 95% confidence limits using two-tailed tests for significance; "n" refers to the number of experiments used to compute means. Mean rates of compensatory buoyancy change are not significantly different for positive and negative animals during the first 10-h intervals, but then change. Animals made positively buoyant appear to have a limited compensatory response, as indicated by the significant drop in buoyancy change during the second and later 10-h increments.

computed. These figures are shown in Figure 4 along with the number of observations for each value. The highest rate of weight change occurred during the first 10 h (0.15 g/h) for the 15 specimens used in the experiment. The following 10-h increments had significantly lowered rates of weight change; the second 10-h period showed rates of about 0.05 g/hour. Subsequent 10-h periods showed similarly lowered rates. These experiments suggest that the greatest amount of compensatory buoyancy change will

occur within the first 10 h, and that subsequent change will be far less.

A second group of experiments was designed to examine the relationship between rates of compensatory buoyancy change in response to increased buoyancy and the amount of buoyancy change initiating the response: does an ever higher initial buoyancy change produce ever faster compensatory changes in response? To test this, the initial amount of induced weight change was plotted against

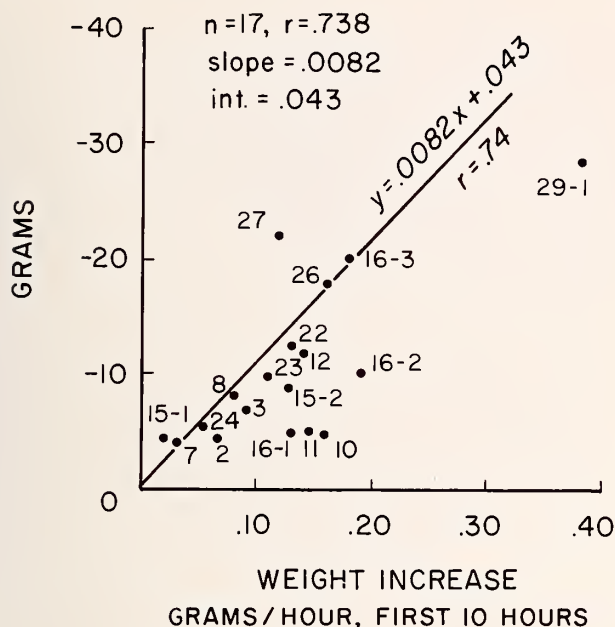


Figure 5

Relationship between rate of compensatory buoyancy change in animals made suddenly positive, against amount of positive buoyancy initiating the experiment. There does appear to be some positive correlation between the rate of compensatory refilling response and the amount of buoyancy increase at the start of the experiment. Previously, GREENWALD *et al.* (1980) and WARD (1982) have shown that a similar relationship exists between the opposite conditions, *i.e.*, liquid emptying rates and initial *negative* buoyancy.

compensatory response for the first 10 h (Figure 5). The correlation coefficient for the linear regression is 0.738. Apparently the initial amount of buoyancy change does affect the rate of compensatory response.

The ultimate amount of compensatory buoyancy change was limited. The maximum weight change observed was an increase of 6.5 g (No. 27), and the mean amount was slightly less than 4 g. From these experiments, it appears that the compensatory response to suddenly increased buoyancy is, at least at surface pressure, extremely limited, and in this species probably never reaches as much as 10 g, regardless of the initiating buoyancy change.

#### Induced Buoyancy Change: Decreased Buoyancy

Experiments examining liquid emptying rates in response to buoyancy change have previously been made by GREENWALD *et al.* (1980) and WARD (1982a). Compensatory buoyancy change in nautilus specimens made heavy by the addition of cameral liquid to partially or completely emptied chambers, or through the addition of weights to the side of the shell, was monitored in a fashion similar to that used for nautilus made artificially less dense. The heavy nautilus were weighed in seawater at 30-min to 2-h intervals, and the aggregate amount of weight change

recorded. The results of these experiments are shown in Figures 6-7.

As in the case of artificially increased buoyancy, the animals made suddenly heavier than seawater showed compensatory buoyancy change. The rates of weight change during the first 10 h for the nautilus made heavy were not significantly different from the rates of decreasing buoyancy change for the nautilus made light, as described above ( $-0.10$  g/h for the first 10 h, as compared to  $0.15$  g/h for the nautilus made light). Unlike the experiments with nautilus made lighter, however, these specimens showed roughly similar rates of weight change during the following 10-h intervals (Figure 4). During the second 10-h period, rates were higher than during the first 10 h ( $0.13$  g/h). Subsequent rates per 10-h increments were variable, but never significantly different. Compensatory buoyancy change following sudden buoyancy decrease thus seems different from that following sudden buoyancy increase.

#### The Mode of Buoyancy Change

In both cases described above, the question of the mechanism involved must be considered. It has been demonstrated that buoyancy change can be effected in a nautilus through the movement of liquid out of, as well as into, chambers (WARD & MARTIN, 1978; GREENWALD *et al.*, 1980; WARD & GREENWALD, 1982). The nature of the weight-change curves in the experiments described here, however, suggests that the mechanism is more complex than the simple removal or addition of liquid from reservoirs of liquid pooled at the bottoms of the last several chambers.

To examine the nature of the buoyancy change system, the amount of cameral liquid in each experimental animal was measured prior to the initiation of each experiment. Each nautilus was radiographed, and those specimens with visible pooled liquid within their chambers were drilled. As in previously reported cases with mature nautilus specimens, the presence of pooled water was usually found only in the last one or two chambers; it has been shown that mature nautilus characteristically contain little or no cameral liquid (COLLINS *et al.*, 1980). In the cases where nautilus specimens were made heavier through the addition of new cameral liquid into the last one or two chambers, the original chamber volume was also noted, so that the new chamber volume at the start of the experiment was known. Through repeated experiments of adding or removing liquid into chambers, it was found that experimental error in volume measurement using this technique was within 0.2 ml of the originally implied volume.

If 1 ml of cameral liquid or seawater is assumed to weigh 1 g, then the change of cameral liquid volume should be the same as the change of weight. It soon became apparent, during the course of the experiments, that the weight change of most of the experimental animals ex-

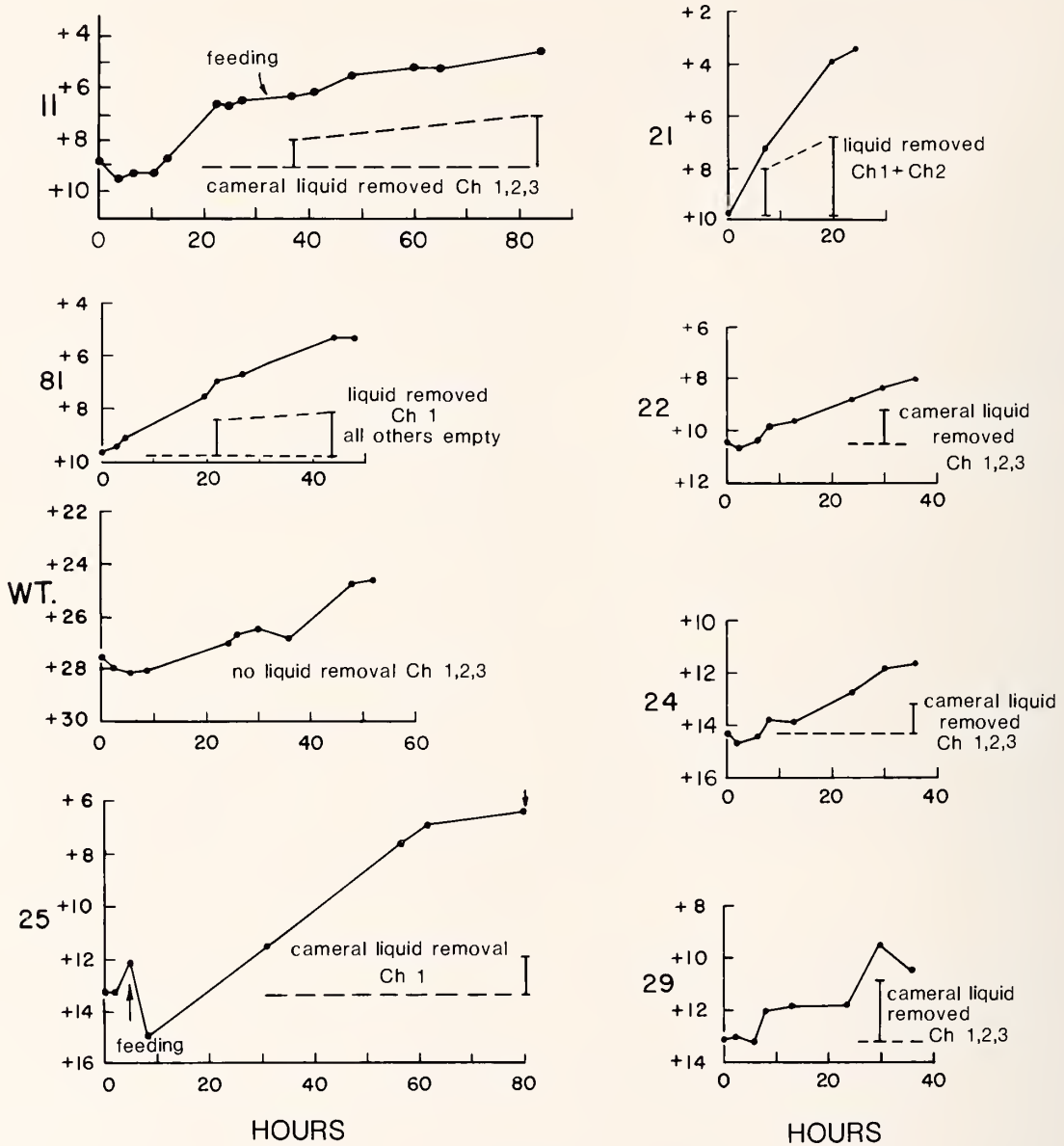


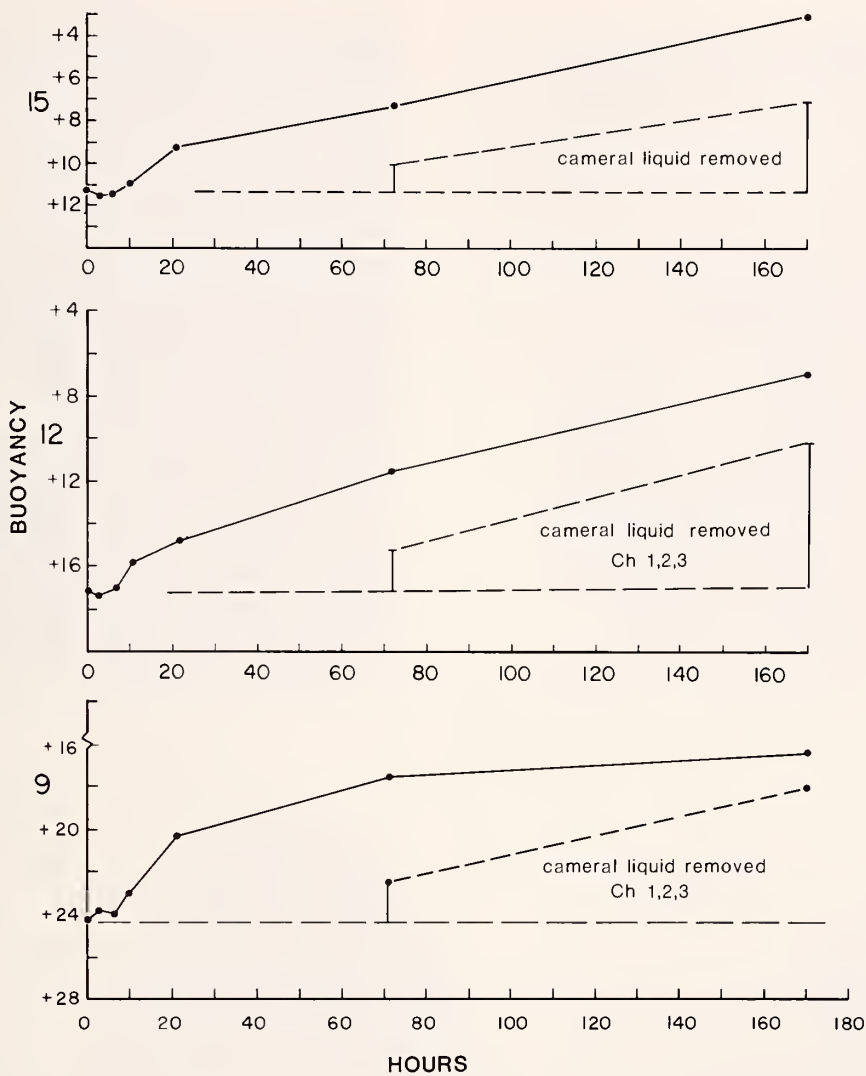
Figure 6

Compensatory buoyancy change in eight *Nautilus macromphalus* made artificially less buoyant by addition of seawater into chambers or addition of metal weights to the shell. The "liquid removed" part of the graph refers to the amount of compensatory buoyancy change that can be attributed to measurable cameral liquid removed.

ceeded the measurable volume change of liquid moving into, or out of, chambers. This is best illustrated in the figures showing experimental results. In these figures, known weight change and volume change are shown on the same graph. The figures have been plotted so as to show the amount of weight change attributed to measurable liquid removal or addition in the last two or three chambers. In almost every case, initial weight change was not caused by addition or removal of pooled liquid; instead, changes in the volumes of these liquids within the

last two or three chambers were only seen *after* a duration of several hours. Only two possibilities exist to explain the observed buoyancy change. Either buoyancy change is being affected by density changes within the soft parts of the animal, or density change is occurring within the phragmocone, but in a manner not observable either with radiographs or in chamber volume determinations.

To test for the possibility of density changes occurring in the body chamber, specimens of *Nautilus macromphalus* were made either lighter or heavier in a manner used in



HOURS

Figure 7

Compensatory buoyancy change in three *Nautilus macromphalus* made less buoyant.

the previous experiments. After the confirmation of weight change (through balance measurements) these animals were sacrificed. Samples of blood, coelomic fluid (from the liver region), and a variety of tissue samples were taken (Table 1). In no case could accurate density measurements ( $\pm 0.002$ ) show tissue or fluid densities suggestive of soft-part compensatory response sufficient to account for the observed but unaccounted for weight change. For example, in those animals made heavy, the observed volumes and densities of blood, liver, and coelomic fluid do not appear to be agents of compensatory buoyancy change.

Another possibility is that buoyancy change was occurring within the phragmocone, but not only through the addition or removal of *pooled* liquid (liquid observable on a radiograph as a distinct volume of liquid at the bottom of a chamber) from the last five or so chambers. This

possibility is harder to test for, but is considered to be the cause of the buoyancy change. By breaking open individual chambers, visual observations of the chamber walls indicated that significant volumes of non-pooled water were trapped within the nautilus shell. Most of this appears to be within the pellicle, a hydrophilic membrane that lines the inside of the chambers and covers the outer region of the siphuncle. The chalky layer of the siphuncle could also be a significant reserve of liquid. Also, the use of high-energy radiographic techniques (in contrast to the small, low kv portable machines used in my previous studies) allowed the first observations of the interiors of chambers in the early whorls. Previously, chamber liquid could only be radiographically observed in the last-formed 10 or 11 chambers (chambers of the last whorl). By combining high-energy exposures with high-contrast screens,



technicians at the Radiographic Facility of the Magenta Hospital, New Caledonia, succeeded in penetrating and observing earlier chambers. These chambers showed small but significant liquid volumes, usually trapped at the septal wall-shell wall intersections (the sutures), rather than occurring as pools of liquid at the bottoms of the chambers. These early chambers thus show small volumes of water, long after emptying, in seemingly gravity-defying orientations (Figure 8).

In the event of rapid buoyancy change, it appears that the liquid is moved to or from the pellicle and sutural regions (perhaps in concert with the reservoir contained within the chalky tube of the siphuncle). These volumes are so small (less than 0.2 ml) that movement would not be detected by changes in the volume of "pooled" liquid within the chamber, if any were present. By acting in concert over many chambers, however, this reservoir could produce a significant volume of cameral liquid. For instance, the movement of just 0.1 ml into, or out of, a single chamber would not be measurable by volume determination methods. Produced over 32 chambers, however, over 3 g of buoyancy change would be effected. If this system acts in this way, it may answer the question posed by WARD *et al.* (1980) as to why the siphuncle remains unblocked in life long after earlier chambers have been emptied, and seemingly would be of no further use to the animal's buoyancy system. The chambers, with their thin linings of hydrophilic membrane, may remain active and useful throughout life as a means of allowing "rapid" buoyancy change through admission or removal of small volumes of liquid.

#### Size and Buoyancy Change

If the pellicle system is indeed the source of the rapid, "unaccounted" buoyancy change observed in the experimental animals, it should become increasingly important in increasingly larger nautilus. The amount of buoyancy change allowed by the pellicle system would be dependent on the surface area of the chambers, and thus would be dependent on the number of chambers present. Larger nautilus should be expected to show larger amounts of buoyancy change.

To examine the rates of compensatory buoyancy change

Table 1

Soft-part densities for *Nautilus macromphalus* undergoing compensatory buoyancy change.

Number	Initial buoyancy	Soft-part density ( $\pm 0.002$ )	Digestive gland density ( $\pm 0.002$ )	Coelomic fluid density ( $\pm 0.01$ )
81	negative	1.064	1.073	1.06
21	negative	1.064	1.090	1.03
Wt	negative	1.063	1.070	1.06
25	negative	1.067	1.069	1.06
20	positive	1.068	1.089	1.02
15	positive	1.059	1.081	—
83	positive	1.063	—	—
24	positive	1.062	1.066	1.03
Flt	positive	1.063	1.068	1.04

in differently sized specimens of *Nautilus macromphalus*, immature specimens of various sizes were made between 4 and 7 g positive, and the rate of buoyancy change then was monitored as in the previous experiments. Unfortunately, during these experiments it proved impossible to capture very small *N. macromphalus* (less than 15 chambers); almost all of the specimens used in this study were mature or within one or two chambers of final size.

The list of animals and experiments in which liquid movement was monitored is shown in Table 2. Only three specimens, No. 82-7, 14, and 22, had fewer than 30 or 31 chambers. All three of these specimens showed lowered amounts of "unaccounted" weight change. The two smallest, No. 7 and 14, showed virtually no weight changes. However, it could be that smaller animals were more stressed by the experimental procedures.

#### Buoyancy Change and Depth Equilibrium

The last question examined here relates to the amount of positive buoyancy necessary to drive a nautilus to the surface and block it there, so that no amount of swimming effort allows resubmergence. Six mature or near mature specimens of *Nautilus macromphalus* were made between 6 to 8 g lighter than seawater. With these buoyancies, all

Figure 8

Radiographs of four freshly captured specimens of *Nautilus macromphalus*. These specimens were radiographed with a high-energy hospital radiograph unit, with the use of high-contrast radiograph film in an image enhancement screen. These radiographs provide the first glimpse into the interior whorls. On normal radiographic exposures of nautilus shells, the interiors of only the last ten or so chambers can be observed; earlier chambers are screened from view by shell (whorl) overlap. The high energy radiographs penetrate two separate shell walls, and clearly show the presence of small volumes of liquid in early chambers. Previously, liquid in *Nautilus* was thought to be present in measurable volumes only in the last formed 4 or 5 chambers in juveniles, and one or two chambers in matures. Note the orientations of the liquid in these chambers, at the top of the chambers, caught between the shell and septal walls, rather than at the bottom of the chambers (the radiographs were taken in the living orientation of the specimen and rotated 90% counterclockwise in the figure, so that "up" is to the left).



Table 2

Buoyancy change in *Nautilus macromphalus*. "Unaccounted" buoyancy change refers to buoyancy change that cannot be attributed to water movement into or out of the last 2 chambers.

Specimen number	Total weight (g)	Number of septa	Starting buoyancy	Total buoyancy change (g)	"Unaccounted for" buoyancy change (g)	Percentage of buoyancy change due to "unaccounted"
7	369	26	-4.5	0.5	0	0
9	665	30	+24.0	7.8	4.4	56
12	756	31	+17.0	10.0	3.6	36
14	219	25	-5.0	0.0	0	0
15	705	31	+11.0	8.2	3.5	43
15	—	—	-4.2	0.9	0	0
15	—	—	-8.5	2.0	1.0	50
16	569	30	-5.0	1.7	1.0	59
16	—	—	-17.5	2.8	2.3	82
20	807	31	-9.8	1.0	0.8	80
21	658	31	+10.0	6.4	3.0	47
22	458	28	+10.5	2.5	0.8	32
22	—	—	-12.8	3.6	0.2	05
23	709	30	-10.0	2.9	0.4	14
24	688	30	-5.0	1.3	0.7	54
24	—	—	+14.0	2.4	1.2	50
27	739	31	-20.2	4.8	1.6	33
29	541	30	-29.0	4.0	1.4	35
29	—	—	+13.1	3.5	1.2	34
81	780	30	+9.6	4.6	2.6	56
w+	708	31	+27.5	3.0	3.0	100

$\bar{X} = 1.15$ ,  $SD = 1.1$ ,  $n = 7$ , for unaccounted buoyancy change, with starting buoyancy positive.\*

$\bar{X} = 2.81$ ,  $SD = 1.1$ ,  $n = 8$ , for unaccounted buoyancy change, with starting buoyancy negative.\*

\* Excluding immature animals No. 7, 14, 22.

were trapped at the surface. Each of these animals was then periodically weighed, and its position (on the surface, or submerged) noted. All showed buoyancy reduction. Each nautilus was weighed the first time it was found to be either attached to the wall or swimming so that the entire shell was submerged; the weights at first submergence varied between -3.5 and -5.0 g. It appears that more than about 5 g excess buoyancy is sufficient to isolate a mature *Nautilus macromphalus* on the surface.

## DISCUSSION

The experiments and observations reported in this paper suggest that compensatory buoyancy change occurs in specimens of *Nautilus macromphalus*. The following points are also raised:

(1) Rates of compensatory weight change for positive and negatively buoyant *Nautilus macromphalus* specimens (surface held animals) are not significantly different (although the directions of change are opposite, with one being an increase in weight, the other a decrease in weight) during the first 10 h, but then change. Those animals originally made negatively buoyant (heavier than seawater) continue to reduce buoyancy at approximately constant rates. Those animals made positively buoyant (light-

er than seawater) show marked reduction in buoyancy change after the first 10-h period.

(2) Because of the change in rates in the positively buoyant specimens, the *potential* for buoyancy change is limited in buoyant animals. For the nautilus made more than 5 g positively buoyant, the range in total buoyancy change was found to be from 1.4 to 6.5 g  $\pm$  0.3 g ( $\bar{X} = 3.8$  g). There was no limit of buoyancy change for animals made negatively buoyant. This indicates that the cameral liquid refilling system (in a compensatory response) allows replacement of a limited volume of water in emptied chambers (at the surface), whereas the cameral liquid emptying system has no limitation, as long as there is liquid within the chambers to remove. In mature animals, however, with small volumes of pooled cameral liquid, compensatory responses would be ultimately limited to liquid pooled and liquid tied up in the pellicle, and hence be quite limited as well.

(3) Positive buoyancy of more than 5.0 g is sufficient to trap mature *Nautilus macromphalus* at the surface, so that no amount of swimming allows resubmergence. Negative buoyancy of 5 g, however, does not trap a mature *N. macromphalus* at the bottom. This is probably due to the position and anatomy of the hyponome, which produces water jet propulsion. The hyponome, located beneath the

Table 3

Liquid refilling rates in single chambers at the surface and at depth.

Specimen no.	Depth (m)	Chamber number	Liquid refilling rates $\mu\text{L}/\text{h}$
83-2	0	1	8.3
83-16	0	1	16.6
83-15	0	2	5.0
83-15	0	2	13.7
83-22	0	1	125
83-27	0	1	93
83-24	0	1	12.5
(From WARD & GREENWALD, 1982)			
81-5	0	1	63
81-5	250	1	100
81-5	250	1	21
81-10	0	1	70
81-10	250	1	75
81-20	0	2	54
81-20	250	2	38

tentacles and head region, is not long enough to direct jets of water directly upward, which would push the animal down. The hyponome is much more efficient at pushing the animal off the bottom, as it can jet directly downward.

(4) Compensatory refilling or emptying appears to occur over many chambers, not just the last two or three. There appear to be significant reserves of liquid within the chambers (perhaps mostly maintained in the pellicle) that allow for removal of liquid from chambers that do not have pooled liquid. Conversely, *Nautilus* specimens appear capable of replacing liquid into the phragmocone system, and thus increasing density, without accumulating volumes of "pooled" liquid at the bottoms of the chambers. Also, in contrast to previous observations, significant volumes of liquid exist in early-formed chambers.

In some respects the experiments listed here are artificial. For instance, the rates of liquid removal for nautilus held at the surface are always much faster than those for animals held at depth (WARD & MARTIN, 1978), and, hence, the rate figures found and listed above would probably not be equivalent to those of a naturally occurring nautilus undergoing compensatory buoyancy change at depths greater than 50 to 100 m. The deeper the depth, the slower the emptying. On the other hand, specimens of *Nautilus macromphalus* are commonly encountered at near-surface depths (WARD, 1982b), and in these cases the surface rates found in this study would probably be quite similar. In the case of positively buoyant nautilus, those animals having sufficient shell removed would be forced to the surface. In this case, the experiments performed here would directly model the case in nature. For those animals experiencing sudden positive buoyancy at depth, but still maintaining depth even though positively buoyant, it could be argued that the added force of ambient

pressure would force water into the chambers and, hence, allow more rapid compensatory buoyancy change than found in this study. Unfortunately, the logistics of producing in-water experiments on emptying and refilling are extremely difficult. No data are available about the rates of in-water buoyancy change. However, data about the amount (volume) of liquid volume change through time in positively buoyant nautilus held at depth are available (WARD & GREENWALD, 1982). In five specimens of *Nautilus macromphalus* held at a depth of 250 m for periods of 4, 24, or 168 h after artificially induced positive buoyancy, rates of liquid refilling ranged between 21 and 100  $\mu\text{L}/\text{hour}$ . Similar rates of refilling for single chambers at surface pressure in this study ranged between 5 and 125  $\mu\text{L}/\text{h}$ , while rates listed by WARD & GREENWALD (1982) for surface-held specimens ranged between 54 and 70  $\mu\text{L}/\text{h}$  (Table 3).

Perhaps the most unexpected result of this study was the finding that variable but significant fractions of the ultimate amount of buoyancy change could not be attributed to measurable liquid volume change within the last-formed two or three chambers in most specimens. Non-pooled liquid is that liquid within a chamber that is trapped by the pellicle and within porous calcareous layers of the siphuncular neck and connecting ring. It cannot be shown experimentally that the removal of this liquid (and also the addition of liquid into this system) is the cause of unexplained density change. However, because it can be demonstrated that density changes are not being produced from within the soft parts, there remain only the small-volume early chambers, and the pellicle and other porous regions within the chambers, that could conceivably be acting for liquid storage. During emptying (following initiation of compensatory buoyancy change in response to increased density) liquid must first be removed from the chalky layers of the connecting ring and siphuncular neck, passing quickly and directly into the siphuncular epithelium. As these regions become emptied of liquid, more liquid will be drawn onto them from the contiguously attached pellicle of the septal face. The pellicle itself then draws up liquid from any pooled liquid volume present at the bottom of the chamber. In those chambers where no pooled liquid is still present, the pellicle will apparently be emptied until it is essentially dehydrated. At this time the chamber is no longer of any use in density change. Through simultaneous removal of liquid from the pellicles of many chambers, relatively rapid density change occurs prior to the observable removal of pooled liquid reserves, which in mature animals can only be found in the last one or two chambers if present at all.

The pellicle system must have some equilibrium volume. However, it appears to be able to take up and store additional liquid if necessary. In the experiment in which animals were made suddenly less dense, significant proportions of the density change observed could not be accounted for by the accumulation of pooled liquid in the chambers. Again, because density increase through soft-

part tissue change could not be demonstrated, the observed density change must have been through the movement of liquid from the siphuncle onto the pellicle, where it was stored. Continued addition of liquid onto the pellicle results in saturation and the initiation of pooling at the base of the chamber. Apparently, as much as 2 g of weight increase can occur before measurable accumulation can be noted.

#### ACKNOWLEDGMENTS

This work was supported by NSF PCM 8202891, P. Ward and L. Greenwald, Co-P.I.'s. I would like to thank Dr. Y. Magnier, Aquarium de Noumea, and Dr. Paul de Boisseson, Director, O.R.S.T.O.M., Noumea, New Caledonia, for allowing me laboratory space. Dr. Marc, Radiography, Magenta Clinic, allowed me the use of his fine radiography facility. Mary Graziose did her usual fine job with the photographic plates. Ellen Bailey completed the drafting. Special thanks to C. Ward, M. Cala, and the Captain and crew of MV *Vauban* for help at sea. Dr. L. Greenwald thoughtfully reviewed this manuscript.

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